

Title	A Mathematical Model for Latitudinal Gradient of Forest Species Diversity(Mathematical Topics in Biology)
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Citation	数理解析研究所講究録 (1993), 828: 126-137
Issue Date	1993-04
URL	http://hdl.handle.net/2433/83305
Right	
Type	Departmental Bulletin Paper
Textversion	publisher

A Mathematical Model for Latitudinal Gradient of Forest Species Diversity

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熱帯多雨林で樹木の種の多様性が高いのはなぜか？

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The species diversity of trees maintained in tropical rain forests is much higher than in temperate, boreal, or seasonally dry tropical forests. In this paper, we analyze a mathematical model of tree-by-tree replacement. With the gap formation occurring throughout the year, a season unfavorable for growth causes a peak of regeneration opportunity in the beginning of the growing season. The resulting synchronization of regeneration opportunity jeopardizes the coexistence of many similar species.

1. Introduction

An important unsolved question in ecology is what controls the richness of species of a similar life form living in the same habitat. The problem is illustrated most clearly by the latitudinal gradient of tree species diversity, as tropical rain forests include by far more tree species than temperate forests of the same area. For example, within a research area of 2 ha of the tropical forest at Pasoh, Malaysia (1), there are 1169 individual trees with the DBH (diameter at breast height) larger than 10cm, and they constitute 276 species. Even the commonest species has no more than 5 percent of the total, only 8 species have more than 18 individuals, and 114 species are represented by a single individual. This makes sharp contrast with many temperate and boreal forests, in which one or a few dominant species occupy a large fraction of area.

Among tropical forests where the temperature is constantly high throughout the year, the species diversity clearly decreases with the length of the dry season (1). The species diversity of trees is the highest for tropical rain forests in Borneo, where monthly precipitation exceeds 100 mm throughout the year. The diversity is lower for Amazonian or African tropics, which

have a few relatively dry months, and it is still lower for tropical seasonal forests and savanna woodlands, where there is a clear dry season of several months.

Gause's principle of competitive exclusion states that it is difficult for species similar in life form and resource utilization to coexist stably. However, trees apparently require a similar set of resources, such as light, soil moisture, mineral nutrients, and yet many species coexist within a habitat (2). What prevents one or a few species that are the most effective in competition from eliminating others? Numerous mechanisms have been speculated to explain the species diversity of trees in tropical rain forests (3). The following are some examples (12).

2. Hypotheses Explaining Latitudinal Gradient of Species Diversity

i) **Specialization of Resource Use:** A classical view is that competing species are more likely to coexist stably when they differ in niche, or the resource use pattern, and that the community can maintain a larger number of species if each species is more specialized (4). Unpredictable or fluctuating resource availability in temperate forests may inhibit the evolution of niche specialization, resulting in fewer coexisting species than in tropics (5). Although specialization of tree species with respect to regeneration is important (2, 6, 7), extremely high diversity of tropical rain forests is unlikely to be explained only by the observed degree of niche specialization (8).

ii) **Mode of Disturbance:** Random disturbance not only delays the competitive exclusion between species, but also actively maintains the species diversity (9). Mathematical models that successfully explain the stable coexistence of a large number of species with very similar life form often assume sedentary and long-lived adults and widely dispersing larvae or seeds ("founder control" models of competition for space, (9)), the examples including Hubbell's random drift model and Chesson and Warner's lottery model (10, 11). A single disturbance event such as a fire or a big storm may kill trees over a large area, and cause spatially clumped and temporally synchronized tree regeneration. If large-scaled disturbances are more pronounced in temperate and boreal regions than in tropics, then this may possibly explain the latitudinal difference of species diversity (12).

iii) **Smaller Opportunity for Competition:** According to the survey of field observations and experiments in a variety of plant communities, including fresh water algal communities, species diversity is often the highest in habitats of relatively low resource supply (13). This trend can be explained intuitively as that a slow growth rate reduces the opportunity for competitive exclusion. The idea can be made more rigorous (14). Negative correlation between soil fertility and species richness may explain the latitudinal diversity gradient, because in the

tropical rain forests the availability of nutrients in the soil would be constantly low, as most nutrient resources are likely to be captured by trees (15). In contrast, in temperate and boreal forests, the availability of soil nutrient may have a seasonal peak, due for example to the synchronized defoliation of trees or to snow-thawing, causing temporarily eutrophic environment providing opportunity for a few fast growing species to dominate the community.

iv) Productivity: Species-energy hypothesis postulates that the energy availability may constrain the number of coexisting species (16). Recent comparative studies of forest species diversity over a very large scale have demonstrated a strong correlation between the species diversity and the annual actual evapotranspiration, a very good predictor of primary productivity (17). However the analysis of finer scaled comparisons sometimes reveals negative correlation between plant species diversity and the net primary productivity (13). In addition, no convincing theory is currently available that explains why species diversity should be higher in productive habitats.

v) Specific Herbivores and Pathogens: A large effect of a generalist predator on species diversity of its prey species has often been demonstrated (18). Probably more effective in enhancing species diversity are the parasites, pathogens, and predators that are specific to host species. These cause greater damage when the susceptible host plant is more abundant, producing strong frequency dependence favoring rare species and enhancing the host guild diversity (19). This can explain the latitudinal diversity gradient if pathogens and herbivores are somehow more active in the tropics than in temperate zones. Janzen's prediction that specific predators in the tropics should suppress the recruitment of tree species near conspecific adult trees is sometimes supported (20), but the observed effect is not strong enough to explain the extreme diversity of tropical forests (21).

vi) Evolutionary/Ecological History: Low tree diversity of temperate and boreal forests is sometimes considered as a result of short time since the retreat of the last glacier. However the lineages of trees in temperate and boreal regions and these habitats themselves are old in evolutionary history (13). The rate of speciation may be higher in the tropics than in temperate regions. For example, animal-pollinated tropical trees may experience faster speciation than wind-pollinated boreal forest trees. Habitat fragmentation of tropical rain forests during glaciation is also suggested to have caused genetic differentiation and produced a large number of tropical species.

All the six hypotheses seem to be plausible and are likely to be important in some situation. However we cannot tell which gives the most important mechanism explaining the

latitudinal gradient of tree species diversity. One effective approach is to model each hypothesis or process and to examine theoretically the condition in which that mechanism works.

In the following, we study a mathematical model describing the dynamical changes in a community by replacement of trees. We analyze in particular how species richness decreases with the length of the cold or dry seasons based on a hypothesis that lower species diversity in temperate regions is a consequence of the greater synchronization of regeneration opportunities than in the tropics. We conclude (1) the mere existence of unfavorable season can reduce significantly the diversity of coexisting species. (2) Diversity in the equilibrium community can be high when niche width of each species is broad and resource use is strongly overlapped. (3) Equilibrium community includes several distinct groups of species differing in phenology of regeneration.

3. Model

Chesson and Warner analyzed the lottery model and demonstrated that the temporal fluctuation of recruitment ability uncorrelated between species is able to maintain a high species diversity (11). The condition this requires (called storage effect) is that sedentary adults once successfully settled can survive over time sufficiently longer than the intervals between intermittent favorable periods that give a tremendous success.

Runkle postulated that the storage effect is the basic mechanism for many similar tree species to coexist in a forest (22). Only a small fraction of sites are disturbed each year. Even tropical trees have strong seasonality in fruit production, and this subsequently causes a higher regeneration ability of the species for subsequent months.

Runkle then noted that the temporal pattern of gap formation and the gap size are similar between tropical and temperate forests (23). In seasonal environments, however, gaps created during the unfavorable season (either cold or dry) remain unfilled and increase in number until the beginning of the following favorable season. This produces a synchronized regeneration opportunity for tree species and gives competitive advantage to the species having the peak regeneration ability at the start of the favorable growing season, resulting in a lower species diversity. As the number of cold or dry months per year increases, the peak rate of supply of gaps in the beginning of the favorable season becomes more important and species diversity decreases.

Here we study this hypothesis. The forest is composed of a large number of sites, each of which occupied by a canopy tree. Each year, only a small fraction of sites receive disturbance and the gaps thus created are filled by the species randomly chosen in the

community, considering seasonality of regeneration ability. Let X_i be the fraction of sites occupied by the i th species ($i = 1, 2, \dots, n$). The change of X_i per year is:

$$\Delta X_i = \lambda \left(-X_i + \int_0^T p(t) \frac{\beta_i(t) X_i}{\sum_{j=1}^n \beta_j(t) X_j} dt \right), \quad (1)$$

where λ is the annual rate of disturbance. The inverse $1/\lambda$ is equal to the average turnover time, and is of the order of 100 to 200 years. T is the length of a year ($T = 360$ days) and t indicates day within a year.

Regeneration opportunity $p(t)$ is the distribution of the date at which gaps are available for regeneration. Let b be the length of the unfavorable season (Fig. 1). $p(t)$ is zero for $0 \leq t \leq b$, and it is large for the first two weeks of the growing season, indicating that all the gaps that are accumulated in the preceding unfavorable season then become available for regeneration. Regeneration opportunity $p(t)$ is normalized so that its integral is equal to unity.

The regeneration ability of the i th species ($i = 1, 2, \dots, n$) on day t ($0 \leq t \leq T$) is:

$$\beta_i(t) = \begin{cases} 1 + \cos((t - i T/n)\pi/w), & |t - i T/n| < w \\ 0, & \text{otherwise} \end{cases} \quad (2)$$

which is larger than 1, half-peak height, for the time period of length w . Note that multiplying regeneration ability by a constant does not change the dynamics, Eq. (1). Function $\beta_i(t)$ has a bell shaped curve and the date at which each species has the peak is spaced regularly over the year.

The present model describes competition of plants differing in the phenological aspect of the regeneration niche (2), where species compete for newly formed gaps. According to this interpretation, regeneration opportunity $p(t)$ is the resource supply rate and regeneration ability $\beta_i(t)$ is the phenological niche for the i th species. The parameter w hence indicates the niche width.

4. Equilibrium Species Diversity

The dynamical system Eq. (1) has a unique equilibrium that is globally stable. This can be proved by considering the following function:

$$V(X_1, \dots, X_n) = - \int_0^T p(t) \log \left[\sum_{j=1}^n \beta_j(t) X_j \right] dt \quad (3)$$

which decreases with time as X_1, \dots, X_n change with time t as changing following Eq. (1) and attains the minimum at the equilibrium, it is a Lyapunov function (26). Eq. (3) is a measure of the distance named "Kullback's divergence" between the two distributions over t , $p(t)$ and $\sum_{j=1}^n \beta_j(t) X_j$ (24). Eq. (3) therefore states that the sum of regeneration ability of the species becomes closer with time to the regeneration opportunity $p(t)$, and in the equilibrium, the community species composition gives the best approximation of $p(t)$ in the environment by a linear combination of regeneration ability curves of n species $\beta_i(t)$.

We here examine how much species diversity can be maintained in the equilibrium of Eq. (1), the diversity being measured simply by the total number of species having a positive abundance.

The model analyzed extremely species rich communities with many sparse species that differ very little from each other in regeneration niche. As the total number of species n increases, more species with similar phenology become included, and each species decreases its abundance. The number of species present in the equilibrium community S increases almost in proportion to the total number of species n .

Species diversity versus the length of unfavorable season Fig. 2A illustrates the relationships for the number of species S and the length of unfavorable season b . The total number of species is $n = 80$. The diversity decreases with the length of unfavorable season, as postulated (22). However the way it decreases greatly depends on niche width w .

Species diversity versus niche width Fig. 2B illustrates the relationship of the number of existing species S and the niche width w . The diversity is not monotonically decreasing with niche width w . It decreases with w for small w , takes a minimum for an intermediate w , and then increases again for large w .

A traditional concept of species packing suggests that a larger number of species can coexist if the species are more specialized, and hence it predicts the decrease of the species diversity with niche width w . However, in the present model this holds only for small niche width (Fig. 2B). If the niche of each species is sufficiently broad ($w > 120$ days), the number

of species increases (rather than decreases) with the niche width and with the degree of niche overlapping. This seemingly counter-intuitive result can be understood by considering a limiting case of very flat $\beta_i(t)$, in which the species are similar in regeneration ability, and all the species can be maintained in the system. Competitive exclusion is the most effective when $\beta_i(t)$ has an intermediate width, as one or a few species with the peak regeneration date coinciding with the peak regeneration opportunity in the environment dominate and exclude others.

Phenology of coexisting species Fig. 3 illustrates the phenological patterns of the equilibrium community. The abundance of each species is indicated by a symbol on the date at which its regeneration ability is at maximum.

The species having its peak near the beginning of the growing season suppresses other species with similar peak regeneration dates but not those with sufficiently different peak dates. As a consequence, there appears a wave-like pattern of the abundance of species. For example, Fig. 3A illustrates the case with unfavorable season of five months ($b = 150$ days) and niche width $w = 60$ days. There are three groups of species with positive abundance. The species in the first group have the peak regeneration about 170; the second group, between 240 and 260; the third group, between 320 and 325. The distance between adjacent groups is about 70 to 80 days. As the niche width increases, the wavelength of the pattern increases and the number of groups decreases, and finally there remains only a single peak located in the middle (rather than in the beginning) of the growing season (e.g. Fig. 3B is for $w = 165$ days).

Fig. 3C and 3D are the results when the length of unfavorable season is one month, shorter than in Fig. 3A and 3B. Interestingly, for short unfavorable season and wide niche (Fig. 3D), there are many species having peak regeneration during the unfavorable period. This is because a dominant species with peak regeneration in the middle of a growing season suppresses all the species having peak regeneration close to them.

We also studied the case in which the recruitment ability decreases with the abundance of the species and the case in which there is recurrent reinvasion of species from outside source. The results are qualitatively the same as the basic case studied here.

6. Conclusion

The present study shows the importance of temporal pattern, especially seasonal pattern, of the opportunity for regeneration in understanding the species diversity maintained in the forests (22).

In tropical forests, seasonal variation occurs in arrival of seeds at a site, as there is a clear seasonal rhythm of both fruitfall and seed germination (26). Although most tropical rain forest tree species are present in the understory before gaps are produced, the turnover of stems among the seedling pool is high. For example, Augspurger reported that most seedlings die within three months of germination (27). Hence among tree species there is a seasonal variation of the germination advantage of regeneration rates, allowing their coexistence in a habitat through the storage effect mechanism (11).

On the other hand, the length of period during which each tree species are able to regenerate, probably extends over several months instead of a week or two. Since the niche width in the model, denoted by w , should be much longer than the period for high regeneration opportunity, coexisting species must have considerable niche overlap with each other.

One of our findings in this paper is that a broader niche of each species may result in a larger number of coexisting species with an extreme niche overlap. As illustrated by Fig. 2B, 4B and 5B, the relation of the species diversity and the niche width is not monotonical. The previous understanding about the relation of diversity and niche width was that narrow niche (or specialized resource use) should enhance the diversity of coexisting species (4,5). This is the case when the niche width of each species is short compared with the width of regeneration opportunity in the environment. When the niche width is sufficiently broad, the number of coexisting species increase, rather than decreases, with the niche width. This is because many species can coexist if they are very similar. Huston (14) and Hubbell and Foster (8) stated this as the basic mechanism for numerous tree species to coexist in tropical forests without sufficient degree of specialization.

Compared with other hypotheses explaining latitudinal gradient of diversity, the present model identifies a direct logical connection between species diversity difference and the existence of winter or dry season. A merit of the hypothesis is its simplicity. At this moment, however, we cannot tell which of many possible processes is the dominant factor explaining the observed latitudinal gradient of forest diversity, all six classes of hypotheses listed up before look plausible to us. To model each aspect of the hypotheses and to specify the conditions in which each proposed mechanism works, as we have done in this paper, is probably the most effective approach understanding the basic and general mechanism maintaining biodiversity in natural ecosystems.

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(28) To prove the stability of the dynamics. we consider the Eq. (3) plus $\sum_{i=1}^n X_i - 1$ which is zero because the summation of X_i is unity in Eq. (1).

By noting annual change in X_i is small, the one-year change of V following Eq. (1) is always positive:

$$\Delta V(X_1, \dots, X_n) = \sum_{i=1}^n \frac{\partial V}{\partial X_i} \Delta X_i = - \sum_{i=1}^n \lambda X_i \left(\int_0^T p(t) \frac{\beta(t)}{\sum_{j=1}^n \beta(t) X_j} dt - 1 \right)^2 \leq 0$$

This together with the convexity of function V (i.e. Hessian matrix is negative definite) leads to the conclusion in text.

Figure 1 An illustration of the model. Gaps are formed at a constant rate throughout the year. During the season unfavorable for tree growth with the length b , gaps are accumulated without being filled, and become available for regeneration in the beginning of the growing season. (Top) Regeneration opportunity $p(t)$ is zero during the season unfavorable for tree growth with length b . It has a sharp peak in the brief period at the beginning of growing season and is a low constant afterwards. (Bottom) The peak regeneration opportunity is taller with the length of unfavorable season.

Figure 2 The number of species S with positive abundance in the equilibrium. (A) Horizontal axis is the length of unfavorable season b . The number of species S decreases sharply with the length of unfavorable season b , different lines corresponding to different niche width w . (B) Horizontal axis is the niche width w . The number of species tend to be large both for very narrow and very broad niche, but is the lowest for intermediate niche width w . The length of a year is $T = 360$ days, and the total number of species is $n = 80$. The numerals in the figure is the length of bad season b .

Figure 3 The phenological pattern of species at the equilibrium. The abundance of each species is indicated by a circle on the day at which its regeneration ability is at maximum. Solid circles are for species with positive abundance ($X_i > 0$) and open ones are for species absent ($X_i = 0$) in the equilibrium. Shaded areas are for regeneration opportunity curve $p(t)$. (A) Unfavorable season extends five months ($b = 150$ days), and niche width is $w = 60$ days. The community includes three groups of species differing in the date of peak regeneration. Peak dates are separated about 70 to 80 days (a little longer than w). (B) Niche width is broader ($w = 165$). There is a single peak of dominant species that suppresses all the other species. (C) and (D) are for the cases with a shorter unfavorable season ($b = 30$ days). Interestingly, the community may include many species whose the peak regeneration occur in the middle of unfavorable season.

Fig. 1 Iwasa et al.

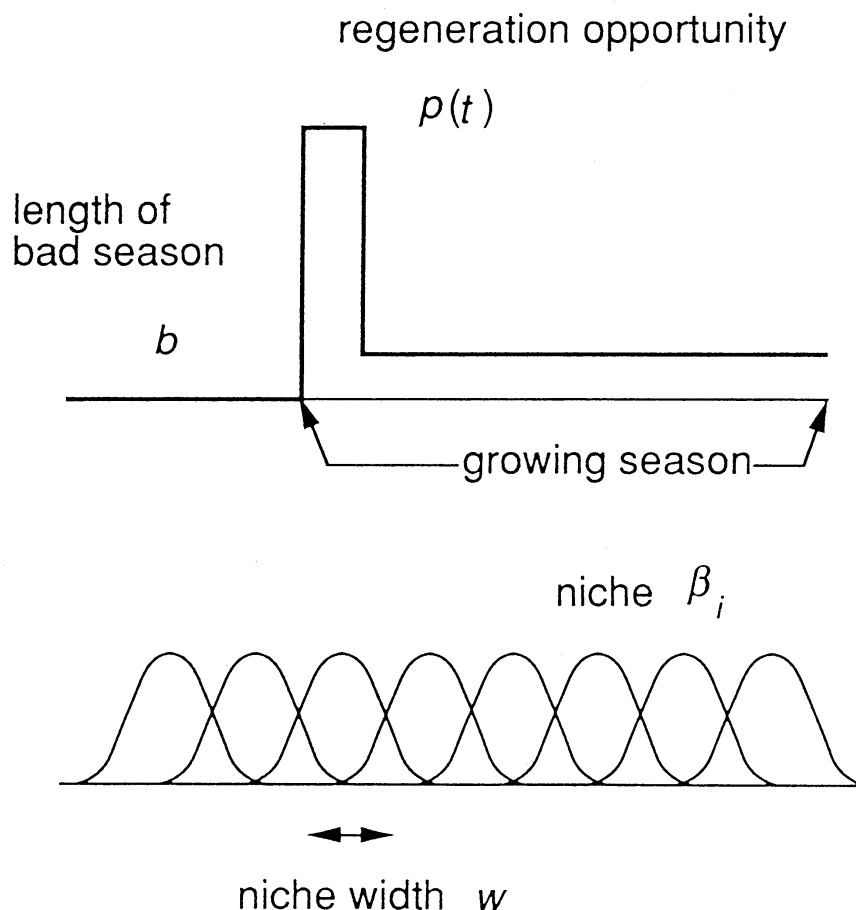


Fig.2

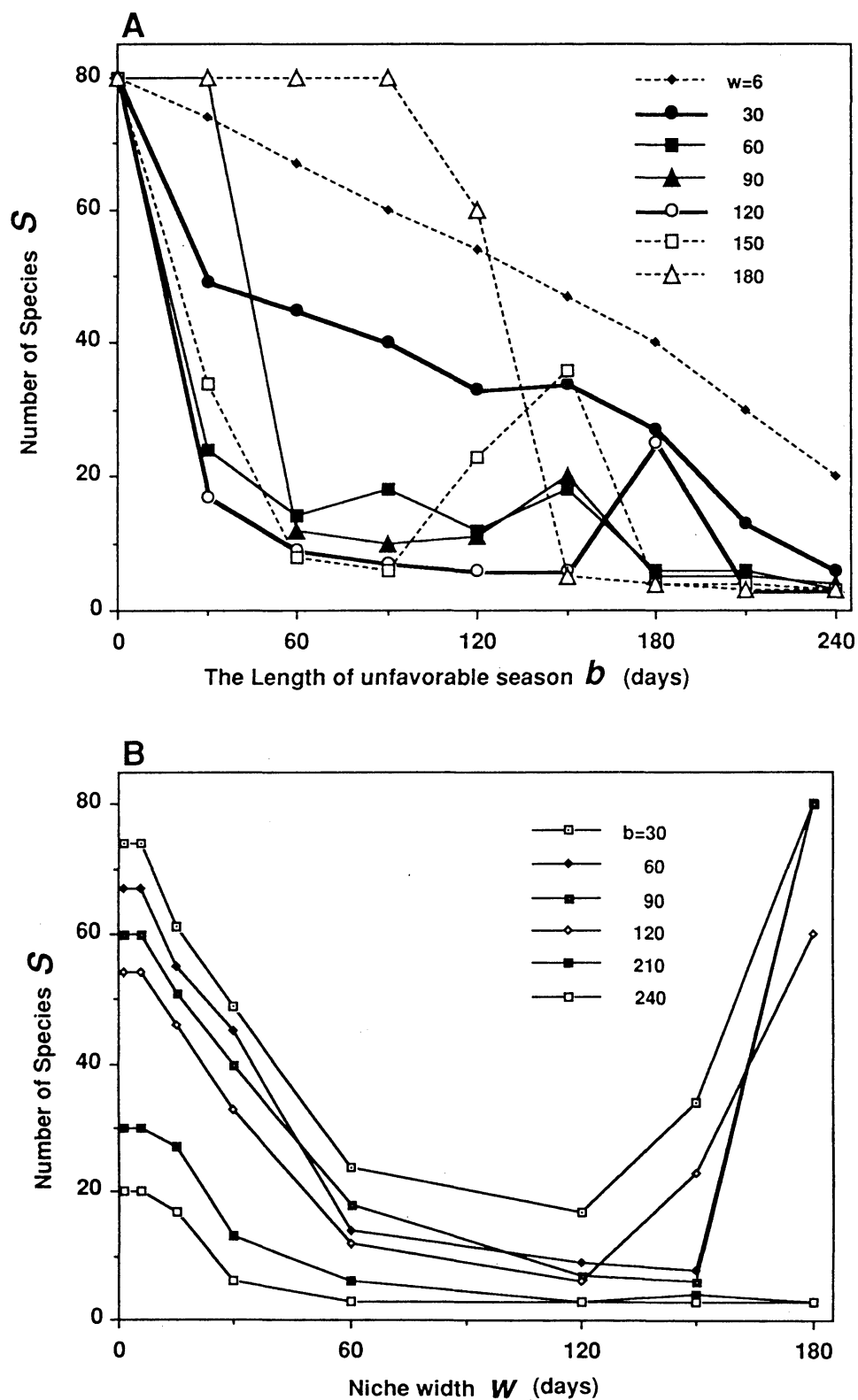


Fig.3

